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Temporal and spatial variation in life history traits of the Japanese gecko, *Gekko japonicus*

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Life-history variation has been widely reported for species with variable clutch size, but detailed data on reproductive strategies for species with invariant clutch sizes are scarce. We collected gravid female geckos (*Gekko japonicus*) from three geographically separate populations to examine geographic and annual variation in reproductive strategies. The majority of females produced a fixed number of eggs ($n=2$). Females from the southern population had larger body size, produced larger eggs, and had heavier clutches than females from two more northern populations, which was largely attributable to among-population differences in maternal body size. Within populations, female body mass varied between years; heavier females laid larger eggs and heavier clutches. The among-year difference in maternal body mass partly accounted for the annual variation in egg size and clutch mass. These results suggest that species with invariant clutch size can adjust egg size to increase or decrease per-clutch reproductive output.

Key words: Annual variation, clutch size, geographic variation, offspring size, reproductive strategy

INTRODUCTION

Life-history traits vary both among and within species, and this variation is likely a reflection of the combined effects of genetic adaptation and phenotypic responses to environmental variation (Stearns, 1992). Identifying life-history variation provides the basis for further theoretical and empirical research on ecological mechanisms and adaptive significance of these patterns. Therefore, life-history variation and its underlying causes are central topics in evolutionary ecology (Stearns, 1992; Stearns, 2000; Roff, 2002; Shine, 2005).

In reptiles, life-history traits differ among geographically separate populations of the same species (e.g., Niewiarowski, 1994; Wapstra & Swain, 2001; Du et al., 2005; Radder, 2006; Zuffi et al., 2007; Qu et al., 2011; Díaz et al., 2012). For example, body size can exhibit substantial variation across geographic clines that conforms to Bergmann's rule in reptiles (e.g., Ashton & Feldman, 2003; Angilletta et al., 2004; Sears & Angilletta, 2004), and is associated with the variation in reproductive traits, with large females tending to produce more and larger eggs (e.g., Bonnet et al., 2000; King, 2000; Du et al., 2005). In addition, life-history traits such as offspring size and number respond to seasonal and annual variation in the environment (Olsson & Shine, 1997; Angilletta et al., 2001; Ji et al., 2007; Du & Shou, 2008; Du et al., 2014). Further studies examining the phenomenon of temporal and spatial variation in life-history traits in response to environmental change will contribute to our

understanding of the ecological and evolutionary forces that may drive the observed variation.

Offspring size and number are key life-history traits that often significantly affect population recruitment and sustainability (Stearns, 1992; Shine, 2005). The classical Smith-Fretwell (1974) model predicts that females reproducing in a given environment should divide available resources into offspring as a result of a trade-off between offspring size and number. This work has inspired numerous studies on offspring size and number in a wide range of taxa with variant clutch (litter) sizes (Ballinger, 1983; Nur, 1984; Shine, 1992; Sinervo et al., 1992; Einum & Fleming, 2000; Roff, 2002). Nonetheless, some lizards (Gekkonidae, Iguanidae, and Scincidae) have evolved invariant clutch (litter) sizes (Shine & Greer, 1991). Because such species lack the ability to flexibly respond to life history trade-offs between egg size and clutch size, or clutch size and clutch frequency, they likely have evolved reproductive strategies uncommon in other squamates (Kratovichil & Frynta, 2006; Kratovichil & Kubicka, 2007; Pike et al., 2012).

In this study, we explore the life-history tactics of a species with invariant clutch size (the Japanese gecko *Gekko japonicus* Schlegel, 1836) in response to environmental variation. *Gekko japonicus* produces clutches typically containing two eggs (Ji et al., 1991; Xu & Ji, 2001; Zhang et al., 2009; Zhu et al., 2009), and we captured gravid females from three geographically and climatically distinct populations spanning the main latitudinal range of distribution for this species (Zhao

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et al., 1999). We focused on the relationships among body size, clutch size and mass as well as egg size and mass to examine intraspecific variation in reproductive strategies. Given their fixed clutch size, we expect that individuals would alter egg size (and therefore offspring size) instead of clutch size in response to environmental variation.

MATERIALS AND METHODS

Study species and animal collection

Gekko japonicus is a small lizard mainly distributed in eastern China, southern Korea and Japan (Zhao et al., 1999). Females are larger than males, and average 61–68 mm SVL (snout-vent length) over their range in China (Ji et al., 1991; Zhang et al., 2009; Zhu et al., 2009). In the Zhejiang Province, female *G. japonicus* lay multiple clutches from May to August (Ji et al., 1991; Xu & Ji, 2001; Zhang et al., 2009; Zhu et al., 2009). However, variation in reproductive life histories across geographic localities remains to be revealed.

In 2013, we collected a total of 446 gravid *G. japonicus* females from three different localities of eastern China: a southern site (Wenzhou of Zhejiang province; 27°8' N, 120°62' E; $n=316$), a central site (Chuzhou of Anhui province; 32°33'N, 118°31'E; $n=46$), and a northern site (Yancheng of Jiangsu Province; 33°38' N, 120°13' E; $n=84$). These populations span the main latitudinal range of *G. japonicus* and experience substantially different thermal environments (Fig. 1). The southern, central and northern females were all collected in between the 6th and 18th May, and laid eggs in 3–8, 2–6 and 3–9 days in captivity, respectively. We also monitored reproductive life histories of the Wenzhou population every year from 2012 to 2015. The sample sizes are 81, 316, 140 and 82 for 2012, 2013, 2014 and 2015, respectively.

Maternal body size and reproductive life history

Females were measured for SVL (± 0.5 mm) and body mass (BM, ± 0.01 g), and were transported to Wenzhou University. Lizards were individually housed in mesh cages (15 cm \times 10 cm \times 6 cm) in a room kept at a constant temperature ($25 \pm 1^\circ\text{C}$) under a light cycle of 12L:12D. A heat source was provided between 0800 and 1600 hours

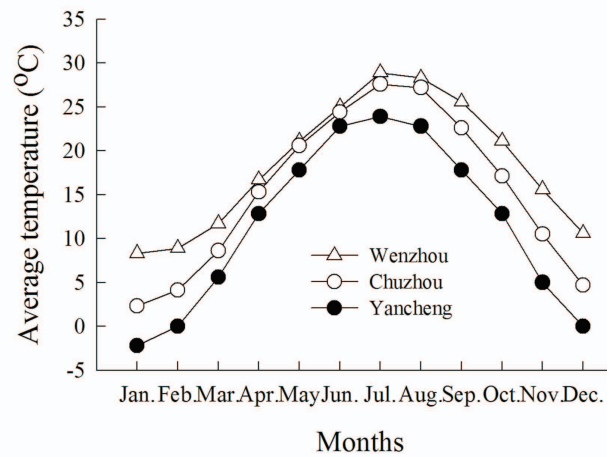


Fig. 1. Monthly average ambient temperatures for the geographic localities where Japanese geckos (*Gekko japonicus*) were collected. Data were obtained from <<http://www.weatherbase.com>>.

to allow for thermoregulation. Food (crickets *Acheta domesticus* dusted with vitamins and minerals and larvae of *Tenebrio molitor*) and water were provided *ad libitum*.

We visually monitored female for gravidity through the semi-transparent abdomen. Females with large oviductal eggs were checked at least three times daily for freshly laid eggs. The total mass of the two eggs was weighed (± 0.001 g) and recorded as clutch mass; mean egg mass was calculated by dividing clutch mass with clutch size. The length and width of each egg was measured using a digital caliper (± 0.01 mm). Maternal post-oviposition mass was also recorded as maternal BM (± 0.001 g). Females were in the laboratory for an average of four days before oviposition (range 3–6 days), and released to their original location of collection following egg deposition.

Statistical analysis

Maternal body condition was quantified with residual scores from the linear regression of \log_e -transformed mass to \log_e -transformed SVL (Schulte-Hostedde et al., 2005; Du, 2006). We used one-way analysis of variance (ANOVA) to detect among-population and among-year

Table 1. The relationship between reproductive traits (clutch mass and egg size) and maternal body size (snout-vent length and body mass) across populations and years in the Japanese gecko (*Gekko japonicus*). Linear regression was used to determine the relationship.

	Among populations		Among years	
	Maternal snout-vent length	Maternal body mass	Maternal snout-vent length	Maternal body mass
Clutch mass	$R^2=0.123$; $F_{1,444}=62.81$, $p<0.0001$	$R^2=0.116$; $F_{1,444}=57.99$, $p<0.0001$	$R^2=0.048$; $F_{1,617}=31.15$, $p<0.0001$	$R^2=0.082$; $F_{1,617}=54.86$, $p<0.0001$
Egg mass	$R^2=0.222$; $F_{1,444}=126.88$, $p<0.0001$	$R^2=0.281$; $F_{1,444}=173.81$, $p<0.0001$	$R^2=0.100$; $F_{1,617}=69.21$, $p<0.0001$	$R^2=0.255$; $F_{1,617}=210.67$, $p<0.0001$
Egg length	$R^2=0.105$; $F_{1,444}=52.12$, $p<0.0001$	$R^2=0.131$; $F_{1,444}=66.74$, $p<0.0001$	$R^2=0.017$; $F_{1,617}=10.72$, $p<0.01$	$R^2=0.046$; $F_{1,617}=29.67$, $p<0.0001$
Egg width	$R^2=0.082$; $F_{1,444}=39.40$, $p<0.0001$	$R^2=0.128$; $F_{1,444}=65.41$, $p<0.0001$	$R^2=0.064$; $F_{1,617}=42.40$, $p<0.0001$	$R^2=0.166$; $F_{1,617}=123.19$, $p<0.0001$

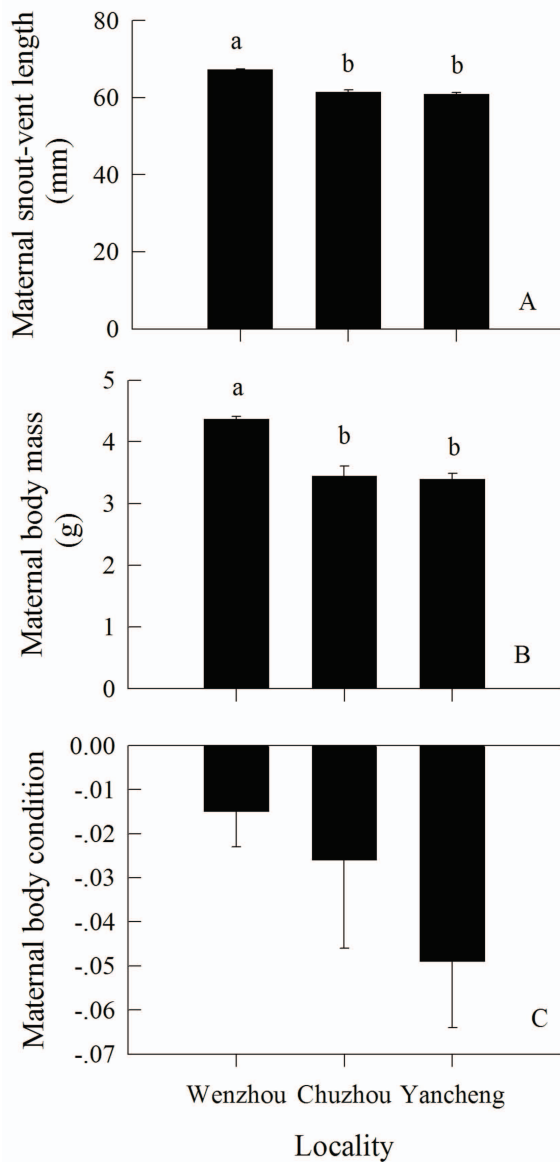


Fig. 2. Geographic variation in maternal snout-vent length (A), body mass (B), and body condition (C) of the Japanese gecko (*Gekko japonicus*). Graphs show mean values ± 1 SE. Means with different letters above the error bars are statistically different (Tukey's test). Sample sizes for the southern (Wenzhou), central (Chuzhou) and northern (Yancheng) populations were 316, 46 and 84, respectively.

differences in maternal SVL, BM and body condition as well as clutch size, clutch mass, egg mass, and egg size (length and width). Linear regression was used to determine the relationship between reproductive traits (clutch mass and egg size) and maternal body size (snout-vent length and body mass) across populations and years. An analysis of covariance (ANCOVA) with maternal SVL as a covariate was also used to detect among-population and among-year differences (in the Wenzhou population) in clutch mass and egg mass and size (length and width). Prior to the ANCOVA, we checked and confirmed the homogeneity of slopes among groups. Tukey's post-hoc multiple-comparisons were used to distinguish among means of traits when the overall analysis was significant.

RESULTS

Geographic variation in reproductive life history

Maternal SVL and BM showed significant geographic variation, with larger geckos in the southern locality compared to the central and northern localities (SVL: $F_{2,443}=124.18$, $p<0.0001$; BM: $F_{2,443}=70.92$, $p<0.0001$; Fig. 2A, B). The post-partum maternal body condition was similar among populations ($F_{2,443}=1.987$, $p=0.138$; Fig. 2C). Most geckos (Wenzhou: 92.7%; Chuzhou: 91.3%; Yancheng: 89.3%) consistently laid two eggs in each clutch and the clutch size did not differ among populations [Wenzhou: 1.93 ± 0.02 ($n=316$), Chuzhou: 1.91 ± 0.04 ($n=46$), and Yancheng: 1.89 ± 0.03 ($n=84$); $F_{2,443}=0.539$, $p=0.584$]. However, mean egg mass and clutch mass were higher in the southern population than the central and northern populations (clutch mass: $F_{2,443}=10.889$, $p<0.0001$; egg mass: $F_{2,443}=19.133$, $p<0.0001$; Fig. 3A, B). The heavier eggs in the southern population were also longer than those from the central and northern populations (egg length: $F_{2,443}=21.880$, $p<0.0001$, egg width: $F_{2,443}=2.881$, $p=0.057$; Fig. 3C, D).

Clutch mass and egg size were positively related to maternal SVL and BM (Table 1). When we used maternal body condition as a covariate in ANCOVAs, the among-population differences in clutch mass and egg size did not change (clutch mass: $F_{2,442}=9.773$, $p<0.0001$; egg mass: $F_{2,442}=17.21$, $p<0.0001$; egg length: $F_{2,442}=20.19$, $p<0.0001$; egg width: $F_{2,442}=1.95$, $p=0.14$). When maternal SVL was controlled for, the among-population differences disappeared for clutch mass and egg size (ANCOVA: clutch mass: $F_{2,442}=0.087$, $p=0.917$; egg mass: $F_{2,442}=0.224$, $p=0.799$; egg width: $F_{2,442}=3.006$, $p=0.051$), but not for egg length (egg length: $F_{2,442}=4.380$, $p=0.01$).

Annual variation in reproductive life history

Maternal SVL did not differ among years in the Wenzhou population ($F_{3,615}=0.041$, $p=0.989$; Fig. 4A), whereas maternal BM and post-partum body condition varied significantly among years. Females were heavier and were in better body condition in 2015 than in other years (2012–2014; BM: $F_{3,615}=14.758$, $p<0.0001$; body condition: $F_{3,615}=27.040$, $p<0.0001$; Fig. 4B, C). Clutch size did not differ among years [2012: 1.86 ± 0.03 ($n=81$); 2013: 1.93 ± 0.02 ($n=316$); 2014: 1.90 ± 0.02 ($n=140$); and 2015: 1.95 ± 0.03 ($n=82$); $F_{3,615}=1.713$, $p=0.163$], but the egg mass and clutch mass were greater in 2015 than previous years (clutch mass: $F_{3,615}=12.407$, $p<0.0001$; egg mass: $F_{3,615}=15.871$, $p<0.0001$; Fig. 5A, B). Eggs in 2015 were also longer and wider than those from previous years (egg length: $F_{3,615}=5.730$, $p<0.001$; egg width: $F_{3,615}=18.577$, $p<0.0001$; Fig. 5C, D).

Clutch mass and egg size were positively related to maternal SVL and BM (Table 1). However, the among-year differences in egg size and clutch mass were not attributable to the difference in maternal SVL alone, because they were still significant when maternal SVL was controlled for (ANCOVA: clutch mass: $F_{3,614}=12.911$, $p<0.0001$; egg mass: $F_{3,614}=17.619$, $p<0.0001$; egg length: $F_{3,614}=5.745$, $p<0.001$; egg width: $F_{3,614}=19.662$, $p<0.0001$).

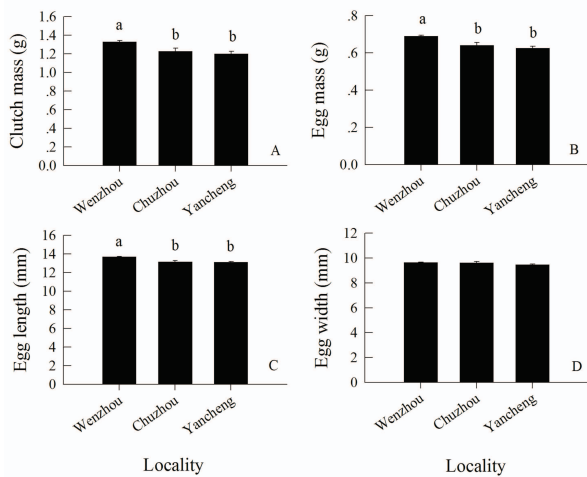


Fig. 3. Geographic variation in clutch mass (A), egg mass (B), egg length (C), and egg width (D) of the Japanese gecko (*Gekko japonicus*). Graphs show mean values ± 1 SE. Means with different letters above the error bars are statistically different (Tukey's test). Sample sizes for the southern (Wenzhou), central (Chuzhou) and northern (Yancheng) populations were 316, 46 and 84, respectively.

DISCUSSION

Our study reveals that egg size and clutch mass of a gecko with invariant clutch size varied among geographically separate populations as well as among years within a population, suggesting that egg size can be adapted to increase per-clutch reproductive output.

Adult body size of many ectotherms vary geographically. Most but not all squamates exhibit a reverse Bergmann's cline (Forsman & Shine, 1995; Ashton & Feldman, 2003; Angilletta et al., 2004; Du et al., 2005; Ji & Wang, 2005; Du et al., 2012; Sun et al., 2013). Similar to most squamates, maternal body size of *G. japonicus* decreases as latitude increases (Fig. 6, see also Ji et al., 1991; Xu & Ji, 2001; Zhang et al., 2009; Zhu et al., 2009). Large body size is likely advantageous due to a positive correlation with between ecological performance and reproductive output (Peters, 1986; Shine, 1988). Large body size in cold climates might result from long periods of growth and delayed maturation, enabling animals to improve per-clutch reproductive output (Partridge & Coyne, 1997; Angilletta et al., 2004; Du et al., 2012). However, environmental constraints such as limited thermoregulation opportunity and low food availability might reduce the body size of ectotherms in cold climates (Sinervo & Adolph, 1994; Du et al., 2000; Sears, 2005). The latitudinal pattern of body size variation in squamates are thus not consistent, and further studies on the underlying ecological and evolutionary driving forces of such variation are warranted.

Geographic variation of reproductive output is widespread in reptiles, which is attributable to both genetic differences and environmental influences among populations (Niewiarowski, 1994; Wapstra & Swain, 2001; Sears & Angilletta, 2004; Du et al., 2005; Ji & Wang, 2005; Shine, 2005). Large body size in the southern population of *G. japonicus* resulted in high

per-clutch reproductive output because egg size and clutch mass were positively related to female body size (both SVL and BM). Our results suggest that geographic variation of per-clutch reproductive output is largely attributable to the differences in maternal body size, because the differences disappeared when the effect of maternal SVL was removed. Maternal body size is an important contributor to geographic variation in reproductive output (Shine, 1992; Kratochvil & Kubicka, 2007). However, the relationship between reproductive traits and maternal body size may differ considerably within and among species. Unlike our case, maternal SVL variation only partially accounts for the geographic differences in reproductive output in many other species (Niewiarowski, 1994; Du et al., 2005; Ji & Wang, 2005; Zeng et al., 2013). For multiple-clutch species, annual reproductive output also depends on the number and

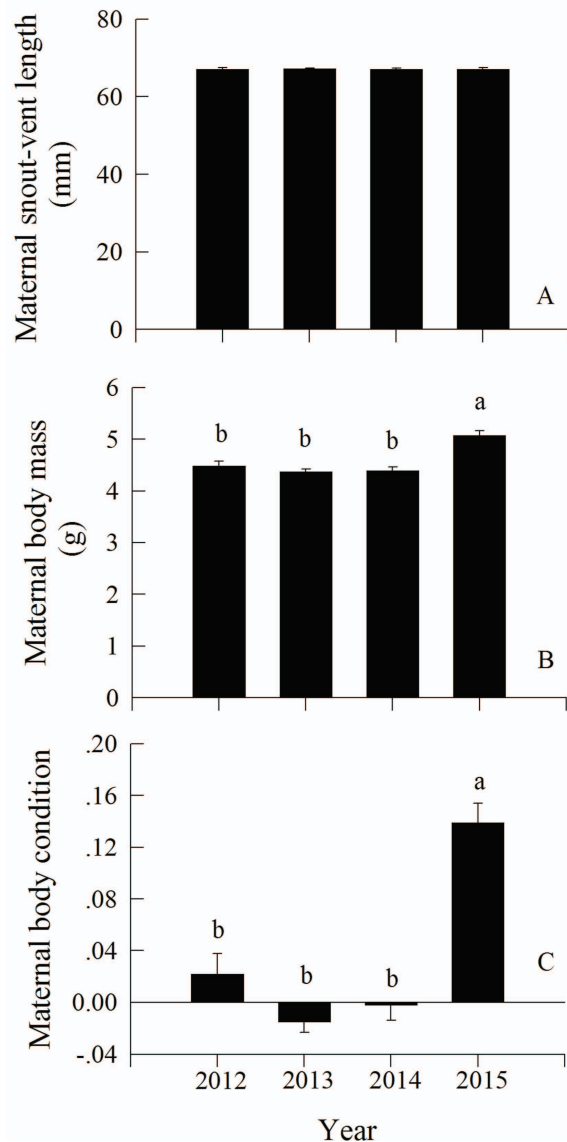


Fig. 4. Annual variation in maternal snout-vent length (A), body mass (B), and body condition (C) of the Japanese gecko (*Gekko japonicus*) population in Wenzhou. Graphs show mean values ± 1 SE. Means with different letters above the error bars are statistically different (Tukey's test). Sample sizes for the years 2012 to 2015 were 81, 316, 140, and 82, respectively.

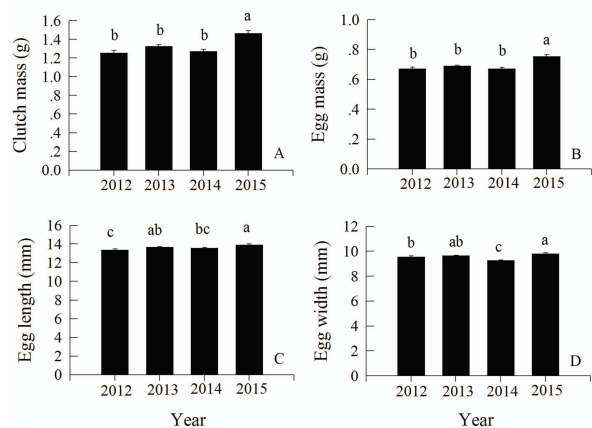


Fig. 5. Annual variation in clutch mass (A), egg mass (B), egg length (C), and egg width (D) of the Japanese gecko (*Gekko japonicus*) population in Wenzhou. Graphs show mean values ± 1 SE. Means with different letters above the error bars are statistically different (Tukey's test). Sample sizes for the years 2012 to 2015 were 81, 316, 140, and 82, respectively.

size of eggs in each clutch as well as on clutch frequency, with a trade-off between offspring size and the annual number of eggs (Warne & Charnov, 2008; Du et al., 2014). Unfortunately, we do not know if *G. japonicus* would show geographic variation in clutch frequency in response to local environments.

In addition to geographic variation, life history also exhibits temporal variation (Ji et al., 2007). The present study showed that maternal body condition varied among years in the Wenzhou population, leading to among-year variation in egg size and clutch mass. In contrast to geographic variation in egg size and clutch mass, the among-year differences in these traits remained different when maternal SVL was controlled for. Such annual variation in reproductive output has also been reported in other reptiles (Olsson & Shine, 1997; Ji et al., 2007), and is likely due to among-year

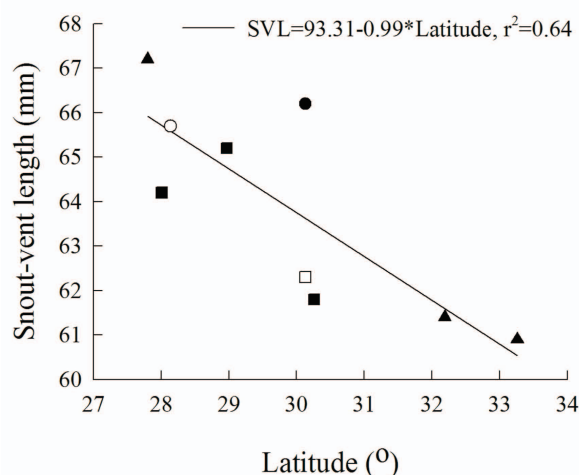


Fig. 6. Average body size of adult female Japanese geckos (*Gekko japonicus*) from nine populations in relation to the latitude. Data were compiled from this study (▲) and additional published literature (Ji et al., 1991 □; Xu & Ji, 2001 ●; Zhang et al., 2009 ○; Zhu et al., 2009 ■).

variation in environmental factors that may affect energy accumulation for reproduction (James & Whitford, 1994; Madsen & Shine, 2000; Du, 2006; Luo et al., 2010).

When allowed to vary, clutch size is often more variable than egg size within and among populations (Du et al., 2005; Ji & Wang, 2005; Sun et al., 2013). Females of species with variable clutch sizes keep egg size rather constant, presumably because optimal egg size provides female with a simple rule to maximize their reproductive success (Smith & Fretwell, 1974; Sinervo & Licht, 1991; Sinervo, 1999). Species with invariant clutch sizes, however, do not have the option of adjust their clutch size. Instead females can adjust egg size relative to body size both among (Pike et al., 2012) and within species (the present study, Table 1), or they can alter their clutch deposition frequency (see also similar studies on anoles, another group of lizards with invariant clutch sizes; Michoud & Echternacht, 1995; Warner & Lovern, 2014; Hernández-Salinas & Ramírez-Bautista, 2015).

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